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Viewer-Centered Object Representation in the Human Visual System Revealed by Viewpoint Aftereffects

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Summary

Are there neurons representing specific views of objects in the human visual system? A visual selective adaptation method was used to address this question. After visual adaptation to an object viewed either 15 or 30 degrees from one side, when the same object was subsequently presented near the frontal view, the perceived viewing directions were biased in a direction opposite to that of the adapted viewpoint. This aftereffect can be obtained with spatially nonoverlapping adapting and test stimuli, and it depends on the global representation of the adapting stimuli. Viewpoint aftereffects were found within, but not across, categories of objects tested (faces, cars, wire-like objects). The magnitude of this aftereffect depends on the angular difference between the adapting and test viewing angles and grows with increasing duration of adaptation. These results support the existence of object-selective neurons tuned to specific viewing angles in the human visual system.

Introduction

Recognizing objects is one of the central functions of human vision. Not surprisingly, understanding how the visual system achieves this important function has been the subject of extensive research. One of the key issues in object recognition is the nature of object representation. Objects viewed from different angles will cast different 2D retinal images, yet we are able to recognize most objects from many viewing angles. Two competing theories of object recognition propose different ways for the human visual system to recognize objects from different views. The so-called viewer-centered theory suggests that this is done based on matching specific views to a set of templates, which requires explicit viewer-specific object representations (Edelman and Bulthoff, 1992; Poggio and Edelman, 1990; Ullman, 1989). The so-called object-centered theory suggests that recognizing objects is based on constructing a structural description of simple parts (e.g., geons), which does not require explicit representations of objects from specific views (Biederman, 1987). The object-centered theory proposes a separate pathway independent of object recognition (potentially a dorsal pathway) to deal with the fact that we can interact appropriately with objects of different views (Biederman and Cooper, 1992; Biederman and Gerhardstein, 1993).

There is no conclusive psychophysical evidence supporting that the human visual system contains neurons that explicitly represent objects in specific views. Previous studies have shown performance costs when human observers learn and recognize objects across rotations in depth (Edelman and Bulthoff, 1992; Bulthoff and Edelman, 1992; Tarr et al., 1998; Troje and Kersten, 1999). However, it was argued that viewpoint-dependent performance is not necessarily an indication of viewer-centered representation; rather, it may “reflect the use of neural paths with different sensitivity en route to the activation of the same representation” (Bar, 2001). On the other hand, neurophysiological evidence can be found that supports either viewer-centered or object-centered representations. In occipitotemporal areas in nonhuman primates, some studies (Perrett et al., 1987; Logothetis et al., 1995; Wang et al., 1996) found neurons responding to objects in a viewpoint-selective manner, and other studies (Logothetis et al., 1994; Booth and Rolls, 1998) found viewpoint-invariant neurons. In the human visual system, Grill-Spector and Malach (2001) used a novel experimental paradigm, functional magnetic resonance-adaptation (fMR-A), to study object representation in the lateral occipital complex (LOC). They found that the LOC is sensitive to changes of viewpoint in that presenting different views of the same object in a temporal block generated a larger BOLD response than did presenting the same view repeatedly. However, with rapid fMRI adaptation or priming paradigms, Kourtzi et al. (2003) and James et al. (2002) found that the LOC responds to objects in a viewpoint-invariant manner.

In the current study, we used adaptation as a tool to explore the nature of object representation in the human visual system. Adaptation is a general property of almost all neural systems. As such, measuring the effects of adaptation has been a time-honored tool of psychophysics due to its power to isolate and temporarily reduce the contribution of specific neural populations. Identifying specific properties that are adaptable has often been used to infer specific mechanisms underlying perceptual processing, from low-level channels to high-level object shapes and facial identity (Kohler and Wallach, 1944; Blakemore and Campbell, 1969; Anstis and Moulden, 1970; Leopold et al., 2001; Suzuki and Grabowecky, 2002). If there are neural populations in the human visual system that are sensitive to different object views, and presumably each group of neurons tuned to a specific viewpoint is adaptable, then one would predict that following an extended period of visual exposure to one side view, a front view will be perceived to tilt toward the opposite direction of the adapting side view (see Figure 1).

Results and Discussion

Three categories of objects were used in our experiment: faces, cars, and wire-like objects. Following a 5 s adaptation to a side-view object and a 2 s blank period, a test object near the frontal view was presented for

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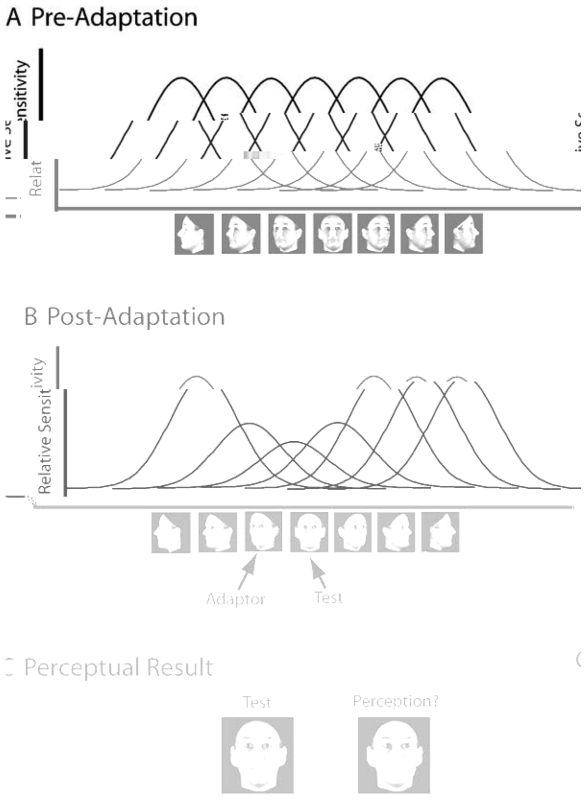

Figure 1. Schematic Depiction of Viewpoint-Specific Adaptation under the Hypothesis of Viewer-Centered Object Representation in the Visual System

(A) A collection of neural populations in the human visual system, each tuned to a particular view.

(B) After adapting to a side view, the sensitivities of neural populations decrease around the adapted viewpoint.

(C) A front view face would be perceived to tilt to the opposite direction of the adaptor if the postadaptation neural sensitivity profile is like that in (B).

0.2 s. Observers were asked to make a two-alternative forced-choice (2-AFC) response to indicate which direction the test stimulus was facing (left or right) (see Figure 2). We chose these three categories of objects because (1) they all have clearly definable facing directions; (2) faces and cars are both familiar objects that have been extensively studied; faces are usually identified at the subordinate level, while cars are usually identified at the basic level (Kanwisher et al., 1997; Gauthier et al., 1997); and (3) the wire-like objects are unfamiliar, and it is easy to manipulate their image properties, providing an excellent set of control stimuli that are two-dimensionally equivalent.

Within each category, the set of stimuli consists of a front view and a number of side views, which were generated by projecting 3D models rotated in depth (clockwise or counter clockwise) into a 2D plane. Since the face and car stimuli have intrinsic front sides, the front views of these two stimuli were defined as the view of their natural front (head-on) side. For the wire-like object, frontal view was defined as the view in which the object appeared symmetrical and with its central components pointing to the observer. Note that the frontal view may or may not be the canonical view of the objects. Side views with small angular rotation (±3 and ±6 degrees) from the front view, along with the front view itself, were used as test stimuli. The side views with large angular rotations (±30 and ±60 degrees for faces and wire-like objects, ±15 and ±30 degrees for cars) were used as adapting stimuli. Since the purpose of the experiment is to examine if there is a viewpoint aftereffect in the human visual system, we sought to avoid the possible confounds due to a conjunction of localized aftereffects for orientation, spatial frequency, and so on. For this reason, the adapting stimuli had a random starting position and were slowly translated in the picture plane in random directions within a confined region, and the positions of the test stimuli were randomly distributed within this area (see Experimental Procedures).

Viewpoint Aftereffect from Side View Adaptation

First we measured how accurately observers could detect the viewing direction of briefly presented test stimuli without any adaptation. Observers made forced-choice responses (whether the test object was facing left or right). The results are presented as psychometric functions with the percentage of "object facing the opposite direction relative to adaptor" plotted as a function of the actual viewing angles of the stimuli. For all three categories of objects, observers gave nearly perfect performances for all five test conditions (50% level for the front view, correct identification for 3 and 6 degree side views in either direction; see blue lines in Figure 3). In other words, observers had no trouble discriminating a viewing angle of 3 degrees from the front view. However, following a 5 s adaptation to the 30 degree side views of faces and wire-like objects and to the 15 degree side views of cars, observers' judgments of viewing directions of the same test stimuli were dramatically different and generally pushed to the opposite direction from the adapted viewpoint. The psychometric function showed a general horizontal shift from the adapted viewpoint (compare black and blue lines in Figure 3). Taking the front view test stimuli as an example, without adaptation, observers were equally likely to see them as facing left or right (50% in Figure 3, blue lines). After adaptation, the front view stimuli were often judged as facing away from the adapted viewing direction. The adaptation effect was strong enough that even some of the test objects that were facing in the same direction as the adaptors were perceived to be facing toward the opposite direction of the adaptors (e.g., following adaptation to a face turned 30 deg to the left, a test face turned 3 degrees to the left was often judged to be facing right; see Figure 3). This perceptual distortion is in sharp contrast with observers' performance without preceding adaptation. This adaptation effect can survive a 2 s blank time between adaptation and test presentation—enough to prevent any perception of motion between adapting and testing stimuli. This "storage" of adaptation over a period of nonstimulation is common for both simple (Mather et al., 1998) and high-level (Leopold et al., 2001) aftereffects.

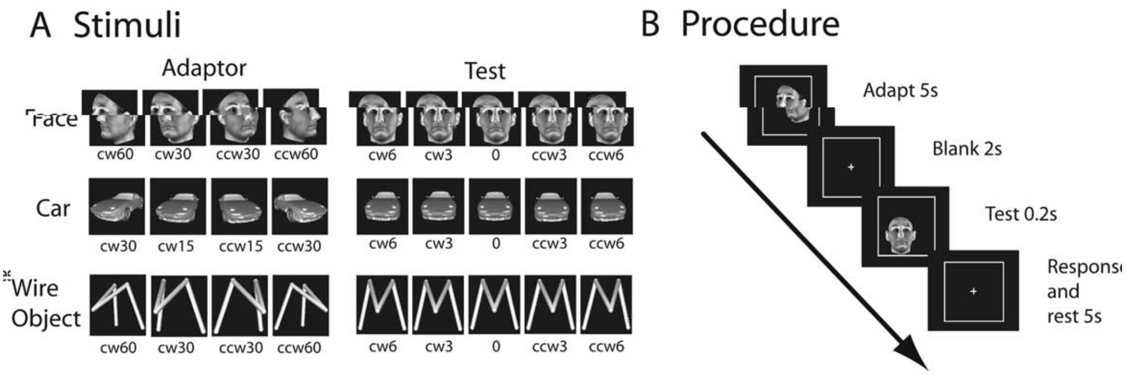

Figure 2. Stimuli and Procedure

(A) Sample stimuli, with schematic depiction of three kinds of stimuli (face, car, and wire-like object) used in the main experiment.

(B) The basic procedure. Adapting and test stimuli were generated by rotating the 3D model in depth clockwise or counter-clockwise.

We termed this perceptual aftereffect a viewpoint aftereffect, implying that it arises due to adaptation of the viewpoint-sensitive neurons. But there are potential alternative explanations. For example, a number of studies have shown that the changes that occur during apparent motion overshoot the location of the “last motion token” (Finke and Shyi, 1988; Nijhawan, 1994). The stimulus flashed last in a multistep apparent motion display sometimes appears as if the motion continued in the mental representation slightly beyond the disappearance of the stimulus. This phenomenon has been called representational momentum. It acts much like physical momentum. In our study, given the angular disparity between adapting and test stimuli, mental rotation might conceivably result from their successive presentations even though the long interstimulus in-

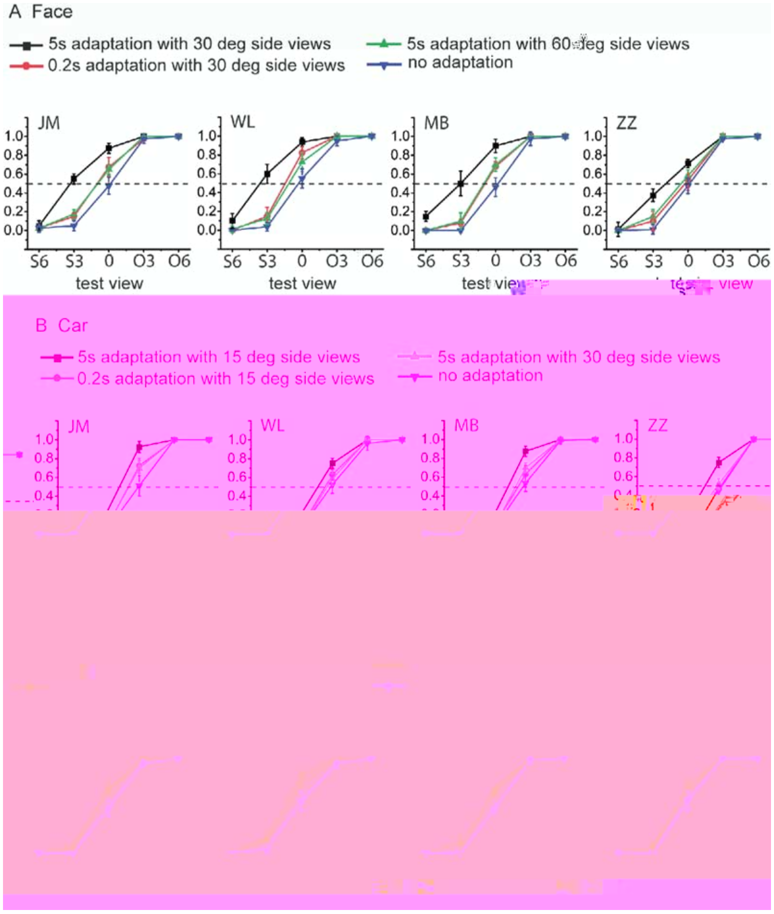

Figure 3. Psychometric Functions Showing Viewpoint Judgments under Different Conditions

Results for face, car, and wire-like object stimuli are presented in (A), (B), and (C), respectively. For all panels, the abscissa refers to the five views of test stimuli. 0 is the front view, and S6, S3, O3, and O6 are side views ±3 or ±6 degrees away from the front view. S and O indicate that the test stimulus has the same or opposite view direction (left or right) as the adaptor, respectively. The ordinate refers to the fraction of trials in which subjects indicated that the viewing direction of the test stimulus was opposite to the adaptor. Error bars denote 1 SD. Conditions depicted with the black lines generated very strong aftereffects; [using subjects’ responses to the 0 degree test as the dependent variable, paired t tests show significant differences between the black conditions and the baseline/blue conditions for all subjects with all three categories of stimuli: Face: $t(3) = 7.375$, $p = 0.005$; Car: $t(3) = 7.185$, $p = 0.006$; Wire-like object: $t(3) = 19.106$, $p < 0.0001$].

terval in our experiments prevented perception of motion. Representational momentum caused by this mental rotation could provide an alternative explanation for viewpoint aftereffect. To test the validity of this explanation, we included a control condition in the experiment in which the adaptation time was reduced to 200 ms. The rationale is that a 200 ms duration of exposure is sufficient to generate representational momentum, but would generate a weaker adaptation effect. If the perceptual distortion of viewpoint following 200 ms adaptation is weaker than that following 5 s adaptation, it would then support the idea that this perceptual distortion can be attributed to a viewpoint aftereffect, rather than to representational momentum. This is indeed what we found [red lines in Figure 3, comparison between 5 s and 0.2 s adaptation; Face: $t(3) = 8.392$, $p = 0.004$; Car: $t(3) = 7.606$, $p = 0.005$; Wire-like object: $t(3) = 7.651$, $p = 0.005$]. It should be noted that high-level shape aftereffects can be induced with a very short adaptation time (Suzuki, 2001). The fact that after 200 ms of adaptation there is still a measurable aftereffect, albeit with much reduced magnitude, supports this [comparison between 0.2 s adaptation and no adaptation, Face: $t(3) = 2.928$, $p = 0.061$; Car: $t(3) = 2.647$, $p = 0.077$; Wire-like object: $t(3) = 4.193$, $p = 0.025$].

Furthermore, inconsistent with the representational momentum, but consistent with viewpoint adaptation is the observation that the magnitude of the viewpoint aftereffect strongly depends on the angular disparity between adapting and test stimuli (green lines in Figure 3). According to the general principle of selective adaptation as depicted in Figure 1, a strong aftereffect can be induced only if there is a significant overlap between neuronal populations responding to the adapting and test stimuli. Differences between adapting and test stimuli that are too small or too big can lead to very weak, or even no, aftereffects at all. In the case of 2D orientation adaptation, direct tilt aftereffect has a narrow orientation tuning, though there could be an indirect orientation adaptation effect occurring at large angular separations (Mitchell and Muir, 1976). We have already shown that 30 degree side views of faces and wire-like objects and 15 degree side views of cars as adaptors can generate a significant viewpoint aftereffect. However, when we doubled these angular differences (60 degree side views of faces and wire-like objects and 30 degree side views of cars as adaptors), observers perceived very weak aftereffects [green lines in Figure 3, comparison between 30 degree and 60 degree adaptation, Face: $t(3) = 18.516$, $p < 0.00001$; Car: $t(3) = 11.263$, $p = 0.002$; Wire-like object: $t(3) = 11.091$, $p = 0.002$]. We also note that due to the overall skewed shape of the car images used for adaptation, the observed aftereffect in car images could potentially arise from a simple 2D shape contrast effect (Suzuki, 2001), in that the skewed adapting image could push the frontal (symmetrical) image to skew in the opposite direction.

The Viewpoint Aftereffect Is Specific to Object Category and Is a Global 3D Effect

Recently, Hinkle and Connor (2002) reported that some neurons in macaque area V4 carry robust signals for 3D orientation defined by binocular disparity. Although the viewpoint in our stimuli was not defined by disparity, the finding by Hinkle and Connor does suggest an alternative explanation for our observation: what we call the viewpoint aftereffect may be a tilt aftereffect in 3D space. The visual system has adapted to the 3D orientation of the adaptor, which then "pushes" the perceived orientation of the test stimulus to the opposite direction of the adaptor. A key prediction of this 3D orientation tilt aftereffect is that it should not depend upon the object category representation in the visual system, as long as the adapting and test stimuli are in the appropriate 3D orientations. To test this prediction, we performed cross-category adaptation experiments. Figure 4 presents the result from one set of the cross-category adaptation, in which adaptors are 30 degree side views of wire-like objects, and testing stimuli are ±6 degree and ±3 degree side views and front views of faces. Compared with the aftereffect from the face stimuli as both adapting and test stimuli (black lines in Figure 4), there is essentially no observable aftereffect from cross-category adaptation (see red lines in Figure 4). Cross adaptation between other pairs of cross-category objects (adapt and test between a face and a car and between a wire-like object and a car) were also tested, and the results are similar to the ones presented in Figure 4. One interpretation of the failure to observe a cross-category viewpoint adaptation is that the viewpoint aftereffect requires rather specific object information, at least at the categorical level. However, because the different object categories contain very different low-level feature properties, the failure to obtain a cross-category viewpoint adaptation effect may also be caused by the dramatically different feature properties. In other words, in order to observe the object viewpoint aftereffect, the adaptor and testing images may have to share a common set of image features. In addition to the cross-category viewpoint adaptation experiments, we also performed preliminary tests using different exemplars within a category—specifically, we used side views of one face as adaptors but frontal views of another face as test stimuli. In this case, there was a viewpoint-specific aftereffect similar to the one for the same faces, but with a slightly reduced magnitude.

Some studies (Suzuki and Cavanagh, 1998; Suzuki, 2001) showed a relatively high-level shape aftereffect—the test shapes always appeared to be more dissimilar to the adapting shape. Shape-tuned neurons in the inferotemporal cortex were proposed to be responsible for this aftereffect. The preceding results provide strong evidence to support the existence of a high-level viewpoint aftereffect. It is still unclear if this aftereffect is a 2D or a 3D aftereffect. In other words, can the viewpoint aftereffect be explained by a conjunction of 2D aftereffects, such as shape aftereffects induced by adapting to 2D image features? The wire-like object offered an excellent opportunity to test whether the viewpoint aftereffect is a 2D or 3D effect. 2D projections from the wire-like object with 30 degree and 150 degree rotations have almost the same 2D features, such as the orientations of bars and their 2D relationship (see Figure 5). However, local T-junction (occlusion cue) manipulation generates totally different 3D interpretations.

This pattern of results suggests that, at least for the simple rire-like objects, the adapting stimuli were represented as 3D objects at the site where this adaptation occurs.

The Viewpoint Aftereffect Requires the Formation of Global Representation: Evidence from Amodal Completion

To further investigate whether the viewpoint adaptation effect is due to adaptation to local features or requires the formation of a global object representation, we took advantage of the phenomenon of amodal completion (Nakayama et al., 1989) and presented identical face patches either behind or in front of occluding visual noise as adaptors. When the patches were stereoscopically presented behind the textured occluder, they were amodally completed and organized into a coherent face by the observer (Figure 6, stimulus 1). When the same patches were presented stereoscopically in front of the textured occluder, they were perceived as disjoint parts (Figure 6, stimulus 2). We found that the former adaptor (amodal completion) induced the viewpoint aftereffect, but the latter stimulus did not (Figure 6). In this case the two adaptors were identical in 2D; the key difference is in the global perception of the face. Adaptation of any 2D feature would predict the same aftereffect from these two adapting stimuli. Our data show a clear and significant difference between these two adapting conditions, which strongly supports the idea that the adaptation is occurring at a relatively high level, where the global object representation has been formed. Adapting to identical local image features without the global object representation is not sufficient to generate the aftereffect.

Theoretical and Physiological Implications

We found that adaptation to a side view of the object had a significant and predictable impact on the perceived facing direction of subsequently presented objects. Our results provide evidence supporting the existence of a viewer-centered object representation in the human visual system. Selective adaptation generally implies neuronal selectivity for the adapted property. Population coding in the presence of an altered sensitivity distribution among competing neural populations following adaptation is generally thought to contribute to the selective aftereffect. Here, the idea is that prolonged exposure to a specific viewpoint could reduce the sensitivity of the corresponding neural subpopulation tuned to the adapted viewpoint.

Although the discovery of explicit viewer-centered object representations will not by itself resolve the long-standing debate between object-centered versus viewer-centered object recognition theorists, it will definitely constrain any theories on object recognition. We should point out that our results do not exclude the existence of neurons sensitive to the structural description of objects or object-centered representations in the human visual system. Both viewer-centered and object-centered representations can coexist. Indeed, a recent study by Foster and Gilson (2002) suggests that object recognition is based on summing signals from two independent processes, one for viewpoint-invariant parts-based processing of 3D object structure and another for the structure-invariant processing of 2D views.

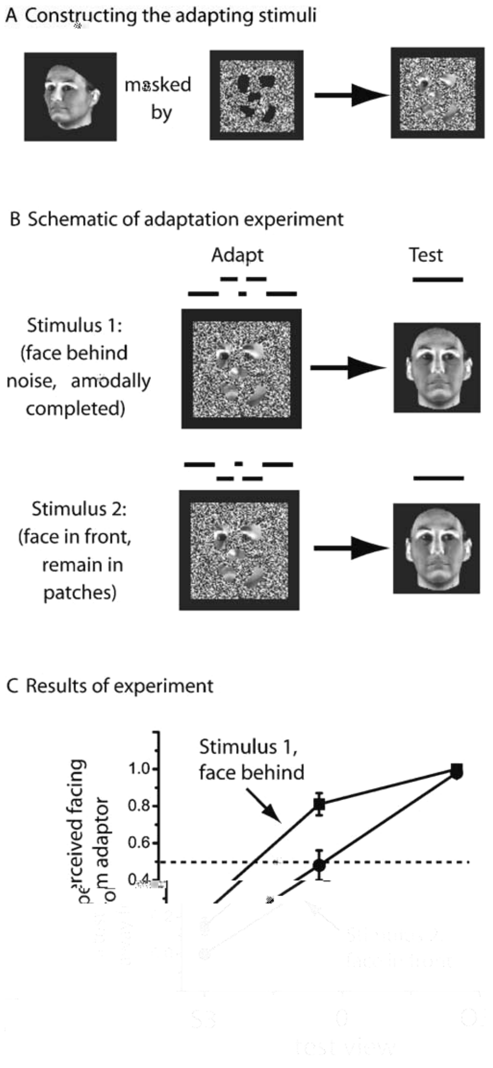

Figure 6. Amodal Completion Experiment

(A) Stimuli construction. The adapting face was masked by a textured occluder, leaving only a few patches visible.

(B) Schematic depiction of the experimental conditions and procedure. When the face patches were behind the textured occluder, a relatively coherent face was seen due to amodal completion (stimulus 1); when the same face patches were presented in front of the textured occluder, the patches remained disjoint (stimulus 2). The key is that stimulus 1 and stimulus 2 are essentially identical in 2D. The test face was unmasked and presented at the same depth plane as the face patches.

(C) Results. After 5 s adaptation, stimulus 2 had no effect on the perceived viewpoint of the test face, while stimulus 1 induced strong and significant change in the perceived viewpoint of the test face [$t(7) = 4.42$, $p = 0.003$]. Data are averaged from eight observers. Error bars represent ±SEM and are computed from means across the eight subjects.

Given the psychophysical evidence for the viewpoint representation, it is natural to ask where in the brain the viewpoint information is represented. A large number of fMRI studies have described focal regions in the occipitotemporal cortex that respond selectively to certain categories of objects: the fusiform face area (FFA) for faces (Kanwisher et al., 1997; McCarthy et al., 1997), the parahippocampal place area (PPA) for places (Haxby et al., 1994; Epstein and Kanwisher, 1998), and the extrastriate body area (EBA) for human bodies (Downing et al., 2001). More importantly, the lateral occipital complex (LOC) was found to be involved in the representation and perception of general shapes and objects (see Grill-Spector et al., 2001 for review). However, until now, there is still no consensus about how these general and specialized object areas represent objects, especially considering the question of viewer-centered or object-centered representation (Grill-Spector and Malach, 2001; Vuilleumier et al., 2002). One potential approach to addressing the issue of neural correlates of viewpoint representation is to use the so-called fMRI adaptation or fMR-A paradigm, but this method is still in its developmental stage. fMRI adaptation was used to demonstrate viewpoint-specific scene representation in the parahippocampal cortex (Epstein et al., 2003). In contrast to the traditional paradigm of adaptation (e.g., relatively long exposure to the adapting stimulus), most existing fMRI adaptation studies used rapid adaptation, which may not be able to distinguish the effects of adaptation from those of anticipated recurrence, novelty/mismatch, or attention (Bentin and Moscovitch, 1988; Nagy and Rugg, 1989). It is now clear that rapid and traditional adaptation methods can produce different conclusions in the primary visual cortex, at least for orientation-specific adaptation (Boynton and Finney, 2003; Tootell et al., 1998). A number of important questions still remain and should be addressed in the near future. First, our results showing

edge of visual adaptation and did not know the purpose of the experiments.

Apparatus and Stimuli

The stimuli were presented on a SONY Trinitron Multiscan G420 19 inch monitor, with a spatial resolution of 1280 × 1024 and refresh rate of 100 Hz. The viewing distance was 57 cm. The adapting and test stimuli were generated by projecting a 3D model with different in-depth rotation angles onto the monitor plane: 15, 30, 60, and 150 degree rotation for adaptors and 0, 3, 6, 174, 177, and 180 degree rotation for test stimuli, with the front view as the initial position. Both clockwise and counterclockwise rotations were executed. The face model is from Max Planck Institute for Biological Cybernetics. The car and wire-like object models were rendered with OpenGL. All the stimuli extend no more than 3.2 × 3.2 degrees.

In the amodal completion experiment, adapting stimuli were generated by masking the 30 degree side view of the face with a textured occluder and were presented stereoscopically by using liquid crystal (LCD) shuttered glasses (StereoGraphics Corporation, San Rafael, CA). Half of the face area of the stimulus was exposed during the adaptation phase. Disparity information specified two depth relations between face patches and the occluder. Face patches were either in front of or behind the occluder. Face patches were always at zero disparity. The occluder was at either +0.17 or −0.17 degree of arc disparity. Test stimuli were whole front views and ±3 degree side views.

Experimental Procedure

Following adaptation, observers were asked to make a response to indicate the view direction of the test stimulus (right or left). During the adaptation period, the adapting stimulus floated randomly within a 5.7 × 5.7 degree area, whose center was coincident with the center of the monitor. Its starting point was randomly distributed in this area, and its floating velocity was 0.85 deg/s. The adaptation time could be 0, 200, or 5000 ms. For the 5000 ms adaptation duration, we monitored fixation stability in two subjects and found that they could maintain their gaze within 1(adaptat82de)-316-314.n69.7o1ue,i

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